

Biophysical Modeling of the Temporal Niche: From First Principles to the Evolution of Activity Patterns

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ABSTRACT: Most mammals can be characterized as nocturnal or diurnal. However infrequently, species may overcome evolutionary constraints and alter their activity patterns. We modeled the fundamental temporal niche of a diurnal desert rodent, the golden spiny mouse, *Acomys russatus*. This species can shift into nocturnal activity in the absence of its congener, the common spiny mouse, *Acomys cahirinus*, suggesting that it was competitively driven into diurnality and that this shift in a small desert rodent may involve physiological costs. Therefore, we compared metabolic costs of diurnal versus nocturnal activity using a biophysical model to evaluate the preferred temporal niche of this species. The model predicted that energy expenditure during foraging is almost always lower during the day except during midday in summer at the less sheltered microhabitat. We also found that a shift in summer to foraging in less sheltered microhabitats in response to predation pressure and food availability involves a significant physiological cost moderated by midday reduction in activity. Thus, adaptation to diurnality may reflect the “ghost of competition past”; climate-driven diurnality is an alternative but less likely hypothesis. While climate is considered to play a major role in the physiology and evolution of mammals, this is the first study to model its potential to affect the evolution of activity patterns of mammals.

Keywords: climate, species activity patterns modeling, golden spiny mice, diurnality, biophysical ecology, microhabitat.

Introduction

Most mammals can be characterized as either nocturnal or diurnal. Activity patterns limited to a specific part of the diel cycle have evolved in response to the time structure of the environment, allowing animals to anticipate the right time for a certain activity or behavior (Daan 1981; DeCoursey 2004). Physical environmental conditions (e.g., solar radiation, relative humidity, wind velocity, and ambient temperatures) that differ between day and night con-

stitute selective pressures that shape physiological and morphological adaptations. Biotic environmental conditions also change between the different diel phases, exposing animals to a different set of ecological interactions (reviewed by Kronfeld-Schor and Dayan [2003, 2008]). Because the anatomical, physiological, and behavioral adaptations that have evolved for diurnal or nocturnal activity differ, they may restrict animals to a certain activity phase (Daan 1981; Kronfeld-Schor et al. 2001a, 2001b, 2001c; Kronfeld-Schor and Dayan 2003, 2008; DeCoursey 2004).

However infrequently, species may overcome these evolutionary constraints and alter their activity patterns (reviewed by Kronfeld-Schor and Dayan [2003, 2008]; Roll et al. 2006) or even lose their rhythmicity (van Oort et al. 2005). The temporal shift in activity patterns may evolve as a response to more suitable climatic conditions in the new activity phase (e.g., Whitford et al. 1981; Lourens and Nel 1990; Kronfeld-Schor and Dayan 2008), as a consequence of biotic interactions such as predation, competition, and food availability (reviewed by Kronfeld-Schor and Dayan [2003]), or in response to a combination of both abiotic and biotic pressures. Climate, biotic interactions, and evolutionary constraints may have similar, different, or even conflicting effects on activity patterns. The selective forces and the evolutionary process involved in such shifts have received little attention and are still little understood.

In recent years, there has been some modeling as well as empirical research on the role of competition and predation in shaping activity patterns (e.g., Brown and Kotler 2004; Kotler et al. 2004; Verdolin 2006; Scheibler and Wollnik 2009; Berger-Tal et al. 2010); there are also an increasing number of studies suggesting that climatic conditions affect preferred activity hours and phases (reviewed by Kronfeld-Schor and Dayan [2003, 2008]). However, to date there has been no effort to model the effects of climate on activity patterns of small mammals. We used a mech-

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anistic approach to study the differences in thermoregulatory metabolic costs under diurnal versus nocturnal activity phases, developing a biophysical model of heat and mass transfer as a function of the microclimate and the physiological and ecological characteristics of the study animal (see Porter et al. 1994, 2000, 2002, 2006).

An excellent model system for the study of the selective forces affecting activity patterns occurs in the rocky Judean Desert in Israel, where two ecologically similar congeneric species of spiny mice have attracted scientific attention (reviewed in Kronfeld-Schor and Dayan 2003, 2008) as a result of their unique temporal partitioning in activity patterns: the common spiny mouse, *Acomys cahirinus*, is nocturnal, as are most desert rodents, while the golden spiny mouse, *Acomys russatus*, is diurnally active (Shargal et al. 2000). Previous studies suggested that the golden spiny mouse was competitively excluded into diurnality by the common spiny mouse (Shkolnik 1971; Gutman and Dayan 2005). Under field experimental conditions, the removal of common spiny mice from the joint habitat enabled golden spiny mouse individuals to also be active during the night (Shkolnik 1971), although their activity remains largely diurnal (Gutman and Dayan 2005). Moreover, most golden spiny mice are nocturnal under controlled laboratory conditions (~86%; Cohen and Kronfeld-Schor 2006), and some individuals show spontaneous temporal shifts in activity between day and night and vice versa (Cohen and Kronfeld-Schor 2006; Gutman et al. 2007; Cohen et al. 2009). In disturbed areas near human settlements, where food availability is high, population densities increase, in particular those of common spiny mice. Therefore, we suggest that food (as an energy and water source) may be limiting in this system under natural conditions (Kronfeld-Schor and Dayan 1999). In the field, both spiny mouse species overlap in their diet composition, with laboratory cafeteria experiments demonstrating a preference for arthropods (Kronfeld-Schor and Dayan 1999). We studied variations in arthropod taxa (species, genera, and families) and biomass in the species' natural habitat and found that more arthropods and greater arthropod biomass were available during the night in all seasons, suggesting that, in terms of resource availability, night should be the preferred activity time for spiny mice.

The golden spiny mouse's legacy as a nocturnal species is reflected in several morphological and physiological adaptations: a high capacity for nonshivering thermogenesis (NST) adaptive for cooler nights (Kronfeld-Schor et al. 2000), a physiological and behavioral response to moon phase in spite of their diurnal activity (Gutman et al. 2011), rod-based retinal structure suitable for night vision (Kronfeld-Schor et al. 2001b), its masking response to dark pulses (Cohen et al. 2010), and an underlying internal circadian rhythm (Levy et al. 2007). However, the overt

activity pattern of this species is diurnal, and it has evolved dark skin pigmentation and a high concentration of ascorbic acid, protecting skin and eyes from solar radiation (Koskela et al. 1989). Moreover, it shows no significant response to light pulses at night, which may reflect a mechanism enabling this species to occupy either a diurnal or a nocturnal niche in its natural habitat (Cohen et al. 2010; Rotics et al. 2011a, 2011b).

Because golden spiny mice remain mostly diurnal even in the absence of common spiny mice (Gutman and Dayan 2005; Levy et al. 2007), it could be argued that diurnal activity in golden spiny mice is the "ghost of competition past" (Connell 1980); diurnal activity has evolved in response to competition to the point where the species is more adapted to diurnal than nocturnal activity. Alternatively, it could be argued that an alternative evolutionary force has selected for golden spiny mouse diurnality. Moreover, it was frequently assumed that golden spiny mice pay a significant price in terms of metabolic costs due to high ambient temperatures during daytime; this hypothesis, however, remains to be tested. Our goal was to model the fundamental temporal niche of the golden spiny mouse and to compare the metabolic costs of diurnal and nocturnal activity.

Climate is an important selective force in desert ecosystems (Shkolnik 1988; Degen 1997). At Ein Gedi, for shade air temperatures measured at a height of 2 m, the average maximum temperature in January is 20°C, and the average minimum temperature is 13°C. In July, the average maximum temperature is 38°C, and the average minimum temperature is 28°C (Jaffe 1988). Being active during the night or during the day, therefore, subjects spiny mice to very different environmental challenges. During summer, diurnal activity implies physiological costs in water turnover and metabolism, while during winter, there may be a greater energetic cost of thermoregulation. We previously found, using doubly labeled water (DLW) in the field, that in summer the energy expenditure of the golden spiny mouse tended to be higher than that of the common spiny mouse, while in winter energy requirements of the common spiny mouse were double those of the golden spiny mouse, which may reflect the cost of thermoregulation during cold nights (Kronfeld-Schor et al. 2001c). Thus, the physiological costs of diurnal and nocturnal activity not only may differ but may vary seasonally.

Studying the role of abiotic factors in shaping activity patterns should involve calculations of the differences between the costs of activity (such as foraging) in the different activity phases in the species' natural environment. Although there are several methods for field measurements of metabolic costs, such as DLW and heart rate recordings, each of these methods has limitations (reviewed by Butler

et al. [2004]); more importantly, none of these methods is appropriate for predicting activity preferences because they measure only the actual metabolism of an animal and cannot predict what it will be at certain hypothetical time points or ranges. We therefore used a mechanistic approach, Niche Mapper, to predict the metabolic costs of golden spiny mice in the field by solving biophysical equations of heat and mass transfer as a function of the microclimate and the characteristics of the animal (see Porter et al. 1994, 2000, 2002, 2006). This method was previously used to predict the climatic constraints on the distribution of mammals (e.g., Natori and Porter 2007), but here we implemented it for modeling the preferred activity phase or temporal niche. We measured the climate at each hour of the day and modeled the metabolic costs of foraging at different hours, in terms of energy expenditure and evaporative water loss required to maintain homeothermy. We discuss our results in the context of the biotic interactions at play in this system and the overall costs and benefits of diurnal versus nocturnal activity.

Material and Methods

In order to predict the metabolic costs of activity during different day parts and climate conditions, the study involved three main components. First, we collected body temperature (T_b) data of free-ranging golden spiny mice individuals and ambient temperature (T_a) data in the microhabitats where the mice almost exclusively foraged. Second, we parameterized the biophysical model according to the golden spiny mouse's morphological and physiological properties and validated it using published data. Third, we used the validated model to predict the metabolic costs in terms of energy expenditure and water loss during each part of the day (see details below).

Field Study Area

The field study took place in Israel, at Ein Gedi Nature Reserve, which is located in a rocky desert near the Dead Sea (35°21'E, 31°27'N, ~300 m below sea level). The study area is located just west of the Ein Gedi Field School of the Society for the Protection of Nature in Israel. Two major habitats are found in the area: a boulder habitat, made up of jumbled rocks up to 2 m in diameter, providing shelter in interstices under and between boulders, and open habitat, characterized by small rocks (pebbles) with occasional isolated large rocks that are usually in full contact with the ground surface and offer no refuge. High vegetation that may provide shade exists almost exclusively near wadi beds or streams in the area or in agricultural areas. To allow individual identification, all spiny mice in the study area were implanted with passive integrated tran-

sponder (PIT) tags. We began trapping and marking golden spiny mice 3 months before data collection in an 80 × 300-m area.

Monitoring Activity T_b and Microhabitat T_a

Body temperature variation is a key means of altering energetic and water requirements and one of the most sensitive variables in heat- and mass-transfer models of animals in their environments (McClure and Porter 1983). The data enabled us to determine the regulated activity T_b in summer and winter, which is an important factor for the model calculation. A week before the beginning of each season's field study, all captured mice (summer, $n = 6$; winter, $n = 8$) were implanted with temperature-sensitive radio transmitters and were released after 48 h. We successfully monitored T_b of five individuals during summer and six individuals during winter. Each implanted radio transmitter uses a unique frequency, which enables individual identification. The transmitter uses a comparison circuit against which to reference the pulse period being determined by the temperature. We used an RX-900 scanner-receiver (Televilt LTD) connected to two dipole antennas for data logging. The receiver scans each frequency for a period of 60 s, and whenever a signal is received, the time, frequency, pulse interval, active antenna, and signal strength are logged. Implanted transmitters were calibrated in a water bath before implementation to the nearest 0.1°C using a precision mercury thermometer. We converted the pulse period to a temperature using the calibration curves we produced using five different temperatures between 25° and 42°C.

We used artificial foraging patches to measure the foraging times and associated body temperatures. We used plastic trays containing 2 g of broken sunflower seeds mixed in 2 L of sifted local sand (Jones et al. 2001; Mandelik et al. 2003; Gutman and Dayan 2005) as foraging patches. We placed the patches in two microhabitats: the under-boulder (UB) microhabitat, which is surrounded by boulders from all directions, including from above, and the between-boulder (BB) microhabitat, which is also surrounded by boulders but does not offer any overhead cover (fig. 1). We positioned the foraging patches in four stations ~60 m apart from one another and located where most of the mice were repeatedly trapped. Each station contained two patches, one in the UB and one in the BB. The activity of marked individuals was recorded using transceivers (Destron Fearing, model 2001) with the antenna of each transceiver located under each foraging patch. When a marked mouse entered a patch, its PIT tag identification code was logged with the exact time of entry. In order to measure T_b at the time of foraging, we located the RX-900 scanner-receiver dipole antennas near each

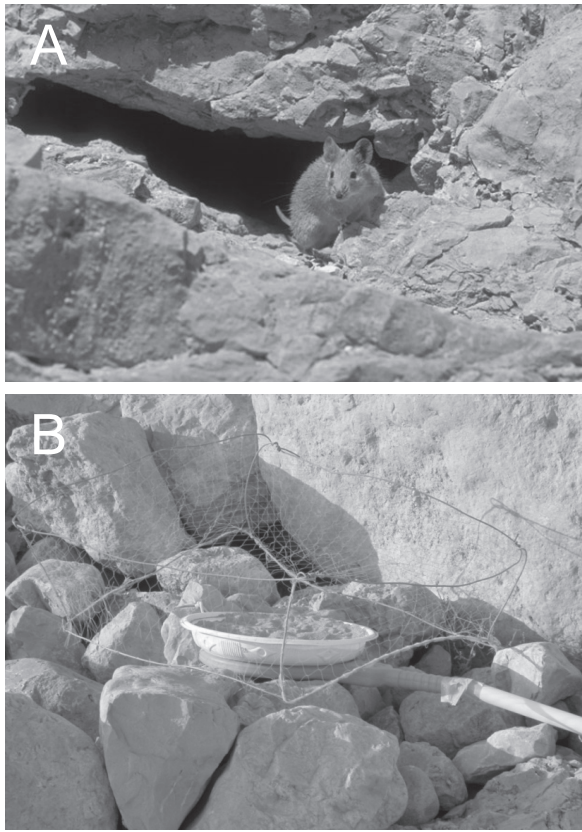


Figure 1: A golden spiny mouse in the under-boulder microhabitat (A) and a foraging patch located in the between-boulder microhabitat (B). The foraging patches included a plastic tray with 2 L of finely sifted local soil and broken sunflower seeds mixed thoroughly together. The activity of marked individuals was recorded using transceivers with the antenna of each transceiver located under each foraging patch. Frames constructed from heavy wire and fine-filament fish netting kept birds out of the trays during the day. Photographs by E. Bartov (A) and E. Vidan (B).

patch station. Using the time and date, we were able to determine the T_b of each foraging mouse.

The T_a was measured to the nearest 0.5°C every 15 min using eight data logger thermometers (iButton ds1921 thermochrom). Each thermometer was placed in a shaded location on the ground, ~ 10 cm away from a foraging patch, four in the UB and four in the BB microhabitats. In the model we use the mean for each microhabitat.

Predicting Day and Night Foraging Costs

We used the Niche Mapper model system (for a detailed description of this model, see Porter and Mitchell 2006), which contains two submodels: a microclimate model and an endotherm niche model. Both models use numerical

methods to solve the heat and mass balance equations for each hour for the environment and the animal of choice. One of the output parameters for endotherms is metabolic rates that would allow the homeothermic animal to maintain its core temperature given the current local available environmental conditions. The details of the animal energetic model have been described by Porter et al. (1994, 2000, 2002, 2006) and by Natori and Porter (2007).

Microclimate Model. We used the microclimate model to predict seasonal climate conditions (wind velocity, relative humidity, and solar radiation at the animal's height) at hourly resolution for each microhabitat. These conditions, together with actual T_a measurements at each microhabitat, were then used by the endotherm niche model to calculate energetic requirements. The model used monthly mean daily minimum and maximum values as input (see table A1, available online). It includes a subroutine for computing clear sky solar radiation given specific shade conditions, time, latitude, longitude, elevation, slope, and aspect (McCullough and Porter 1971). We chose a geographic coordinate at the center of the study site as representative latitude and longitude coordinates. We set the shade conditions at the UB microhabitat as constant 100% and at the BB microhabitat as constant 0%. The shade variable represents the percent of shaded area at the habitat, which can change the amount of solar radiation reaching the ground or the animal; the shade also gives thermal cover by capturing infrared radiation, which is otherwise lost to the sky. We also set the wind velocity at the UB microhabitat as constant 0 (m/s). Free convection is the dominant convective heat-transfer mechanism in this closed environment. For model calculations in the BB microhabitat we used maximal wind velocity data provided by the Israel Meteorological Service (for 6-h increments) and used the microclimatic model to calculate the expected wind velocity at the animal's height. To test how changes in wind velocity may affect our calculations, we ran a sensitivity analysis, letting the maximum wind velocity vary between 7, the maximal value recorded, and 0.7 (m/s). Thus, we only reduced wind velocity in the sensitivity analysis since there was no point in going above actual measured velocities. Our sensitivity analysis results indicate that behavioral avoidance of wind may reduce energetic costs of activity, but there is no change in the sequences measured; hence there is no reason to expect a shift in preferences between diurnal and nocturnal activity. Air temperature input data were the observed hourly T_a values we recorded at each foraging patch.

Endotherm Niche Model. We used the energetics model (Porter et al. 1994, 2000, 2002, 2006) as a mechanistic model to calculate the animal's rate of metabolism, in

terms of energy expenditure and evaporative water loss necessary to maintain homeothermy, given the environmental conditions to which the animal is exposed. It uses measurable properties of the environment (such as air temperature, wind velocity, and surface reflectivity of the ground) and those of the animal (such as size, body temperature, activity level, and fur depth, density, reflectivity, hair diameter, and length). For all simulations, we assumed that mice are active with an ellipsoid posture ($a = 2 \times b$) and with a fixed, empirically measured activity T_b and at a fixed microhabitat (either fully shaded [UB] or not shaded [BB]). Thermoregulation as a response to heat stress was initiated when the estimated metabolic rate was below the empirically measured activity metabolic rate (0.008 W/g, based on Gutman et al. 2006). During thermoregulation, the sequence of events aimed at regulating body temperature was set as (1) a minimization of the silhouette area exposed to the sun (the default animal orientation was normal to the solar radiation, maximizing exposure to the sun); (2) an increase in flesh conductivity (from 0.4 up to 2.8 W/m/°C); and (3) heat loss by evaporative cooling (cutaneous evaporative water loss and licking fur). We parameterized the model using our own measurements of fur properties and the values found in or estimated from the literature for other properties (see table A2, available online).

We developed a computer program ("Energetic Space" [ENSP]) to calculate the hourly energy expenditure and evaporative water loss by running the endotherm niche model for each T_b between 25° and 41°C and T_a between 5° and 55°C, for each hour and individual that was implanted with a temperature-sensitive radio transmitter.

Endotherm Niche Model Validation. We validated model predictions using data from two previous studies of golden spiny mice (Shkolnik and Borut 1969; Gutman et al. 2006). Shkolnik and Borut (1969) showed how energy expenditure and evaporative water loss change over different T_a conditions, while Gutman et al. (2006) showed how energy expenditure changes throughout the day when mice change activity levels and regulated T_b 's. First, to validate model predictions of metabolic rate under different T_a 's, we simulated three laboratory metabolic chamber conditions with three different T_a 's (20°, 25°, and 30°C), assuming free convection and dry air, and compared model predictions of oxygen consumption and evaporative water loss of resting golden spiny mice to data published in Shkolnik and Borut (1969). Niche Mapper predictions were within the mean \pm SD of the published data (see fig. A1, available online). Second, to validate model predictions under different T_b 's and activity levels with constant climate conditions (T_a of 30°C), we ran the model using three different activity levels and allowed a 2.5°C daily variation in body

temperature as input (Gutman et al. 2006) and compared model predictions of oxygen consumption to data published in Gutman et al. (2006). Model predictions were in accordance with the published data of both oxygen consumption and activity level in the laboratory (the laboratory mice were active mostly at the beginning of the dark phase; see fig. A2, available online).

Data Analysis

We inserted the field data and ENSP predictions into a database (MySQL, ver. 5.1) for further analysis. We calculated the mean activity T_b of each golden spiny mouse that entered our artificial foraging patches. We also calculated the mean hourly T_a for each microhabitat at each season. We used Sql queries to determine the metabolic costs, in terms of energy expenditure (mW/g M_b) and evaporative water loss (mg H₂O/s/g M_b , where M_b is body mass) during foraging by hour, microhabitat type (UB/BB), mean hourly T_a , climate data predicted by the microclimate model (wind velocity, relative humidity, solar radiation), and activity T_b for each golden spiny mouse. This data set was used to calculate the mean metabolic costs during daytime and nighttime.

We statistically tested whether the predicted metabolic costs during foraging differ between seasons (summer/winter), habitats (UB/BB), and day parts (day/night). We used mixed-effects ANOVA, with season, habitat, and day part as the fixed factors, individuals as the random factor, and either energy expenditure or evaporative water loss as the response variable. Bayesian inference was chosen because of the observational nature of the study (Anderson et al. 2000). We ran the statistical models using a Markov chain Monte Carlo (MCMC) simulation implemented in the JAGS computer program (Plummer 2008). Noninformative priors were used for all model parameters. We used the R CODA software package (Plummer et al. 2009) to calculate parameters' estimation (with standard deviations and 95% confidence intervals [95% CIs]) and to test their convergence (by convergence criteria described in detail in Cowles and Carlin 1996 and in Mengersen et al. 2000). All results are presented as mean \pm SE or estimate \pm SD.

Results

Field Data

Body mass of golden spiny mice was 42.8 ± 10.1 (g \pm SD) during summer and 43.2 ± 4.7 (g \pm SD) during winter. T_a at each microhabitat showed daily fluctuations and seasonal variation (table 1; fig. 2). Mean foraging activity T_b during summer was $37.5^\circ \pm 0.1^\circ\text{C}$ and during winter was $37.1^\circ \pm 0.2^\circ\text{C}$. Golden spiny mice were re-

Table 1: Shaded air temperatures (T_a) properties ($^{\circ}\text{C} \pm \text{SE}$) measured in the artificial foraging patches

Season and microhabitat	Mean	Minimum	Maximum	Amplitude
Summer:				
BB	$35.4 \pm .6$	$28.4 \pm .4$	45.1 ± 1.3	16.7 ± 1.3
UB	$34.4 \pm .5$	$30.1 \pm .6$	$38.8 \pm .6$	$8.7 \pm .7$
Winter:				
BB	$19.9 \pm .9$	$14.0 \pm .7$	32.6 ± 1.6	18.6 ± 1.3
UB	$19.9 \pm .8$	$15.9 \pm .8$	27.2 ± 1.0	$11.3 \pm .7$

Note: BB = between boulders; UB = under boulders. $N = 8, 4$ at each microhabitat.

corded foraging during all daytime hours in both habitats, except during summer in the BB habitat, where they had a bimodal foraging activity pattern, concentrating their foraging activity in the cooler hours of the day (fig. 2).

Model Predictions for the Cost of Diurnal/Nocturnal Foraging

Model simulations showed hourly fluctuations in energy expenditure and evaporative water loss predictions (fig. 3). Model predictions suggest that during summer, mean foraging activity energy expenditure during daytime was lower than during nighttime in the BB microhabitat (night effect: 2.2 ± 0.7 mW/g M_b) but did not differ from nighttime in the UB microhabitat (night \times UB: -2.2 ± 0.7 mW/g M_b). Energy expenditure in the UB microhabitat was significantly lower by 0.6 ± 0.3 mW/g M_b than in the BB microhabitat. During winter, energy expenditure was higher than during summer at both microhabitats but to a lesser degree in the UB microhabitat (winter effect: 5.9 ± 0.3 mW/g M_b ; winter \times UB: -5.5 ± 0.3 mW/g M_b), and lower during daytime compared to nighttime at both microhabitats (night \times winter effect: 10.7 ± 0.9 mW/g M_b ; night \times winter \times UB: -10.3 ± 0.9 mW/g M_b).

During summer, mean predicted evaporative water loss during daytime foraging activity was higher than during nighttime foraging activity at the BB microhabitat (night effect: -0.014 ± 0.001 mg $\text{H}_2\text{O/s/g}$ M_b) and at the UB microhabitat (night \times UB: 0.013 ± 0.001 mg $\text{H}_2\text{O/s/g}$ M_b). During winter, mean predicted evaporative water loss was significantly lower compared to summer (winter effect: -0.014 ± 0.001 mg $\text{H}_2\text{O/s/g}$ M_b) and was significantly higher during daytime compared to nighttime foraging at the BB microhabitat (night \times winter: 0.013 ± 0.001 mg $\text{H}_2\text{O/s/g}$ M_b), with no significant differences between day and night activity at the UB microhabitat (night \times winter \times UB: -0.013 ± 0.001 mg $\text{H}_2\text{O/s/g}$ M_b). Mean predicted evaporative water loss was lower in the UB microhabitat

compared to the BB microhabitat (UB effect: -0.012 ± 0.001 mg $\text{H}_2\text{O/s/g}$ M_b ; table 2; fig. 3).

Discussion

Diurnal activity in summer in a hot desert is expected to have high thermoregulatory costs. Hence, it could be expected that desert rodents will retain the nocturnal activity pattern, which is also their ancestral state. Indeed, most desert rodents do so, but desert-dwelling golden spiny mice are active during the day.

The endotherm niche model predicted that throughout the year, at both boulder microhabitats tested (under boulders and between boulders), energy expenditure during foraging is almost always lower during the day, with only very minor costs in evaporative water loss. The exception is foraging activity in the less sheltered BB microhabitat during midday in summer, when evaporative water loss rates may increase up to ~ 10 -fold in comparison with nighttime. In accord with these results, we found that in the BB microhabitat during summer, golden spiny mice switched from a unimodal pattern to a bimodal activity pattern and were not active during midday (see also Kronfeld-Schor et al. 2001a). Moreover, we found no significant difference in the rate of water turnover (WTO) between golden and common spiny mice during both seasons, suggesting that golden spiny mice do not pay a greater price in water turnover because of their diurnal activity pattern than do common spiny mice (Kronfeld-Schor et al. 2001c).

Field metabolic rate reflects the costs of basal metabolism, thermoregulation, locomotion, feeding, predator avoidance, reproduction, and other costs. We have recently found that golden spiny mice use torpor as a strategy for conserving both energy and water (Levy et al. 2011a, 2011b). Torpor is used more during winter than during summer; because ambient temperatures are lower during winter, body temperatures drop to lower values ($\sim 26^{\circ}\text{C}$ during winter compared to $\sim 32^{\circ}\text{C}$ during summer), and both result in greater savings in metabolic rate (Levy et al. 2011a). It is possible that the ability of golden spiny

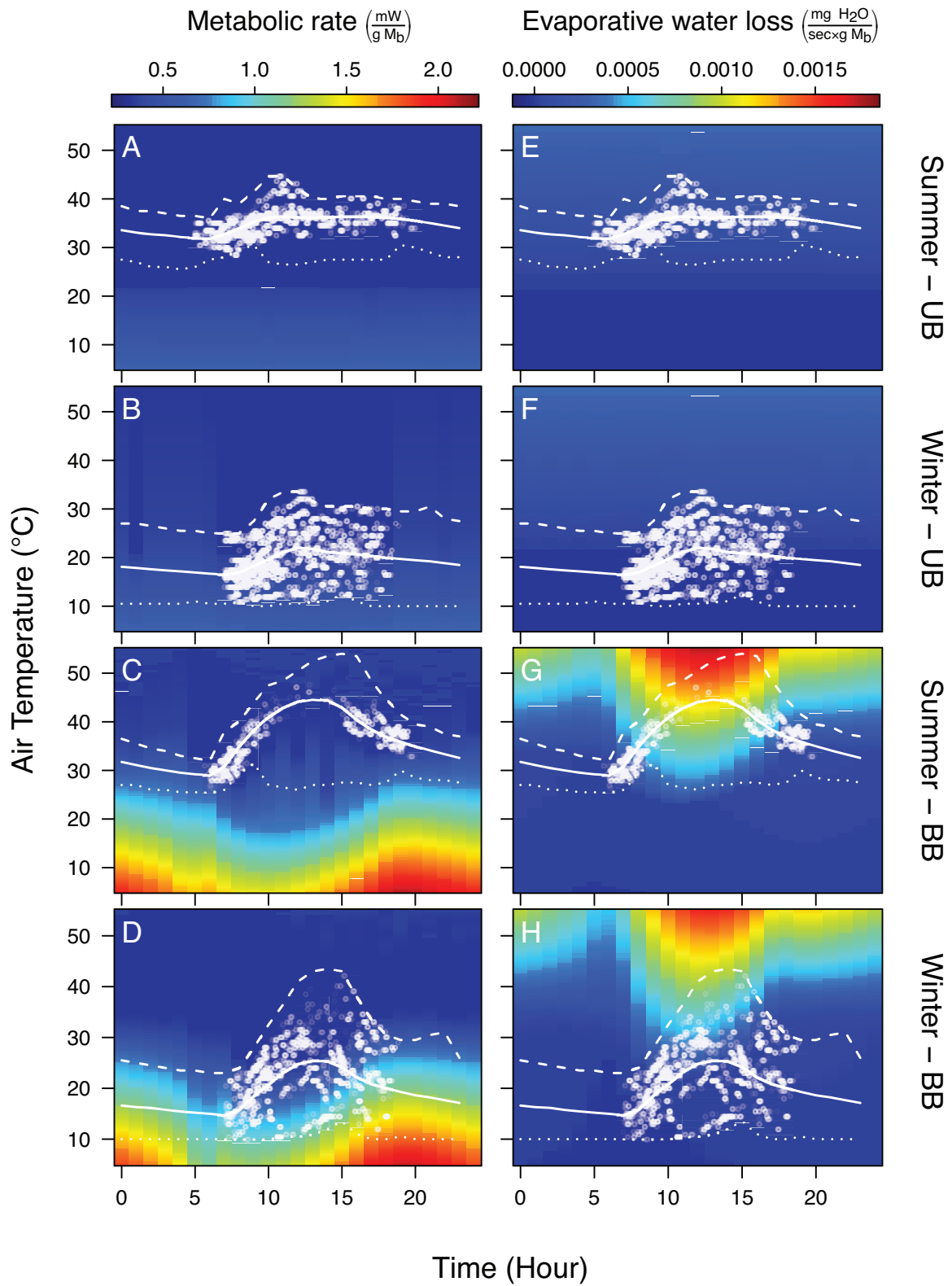


Figure 2: Mean energetic model predictions (summer, $n = 5$; winter, $n = 6$) for hourly metabolic costs of foraging for each hour of the day with T_a between 5° and 55°C. Mean individuals' regulated foraging T_b that we observed in the field was used as the homeothermic set point. White lines represent the thermal niche in each habitat (UB = under boulder, BB = between boulder): solid, mean T_b ; dashed, maximum T_b ; and dotted, minimum T_b . White circles represent the observed foraging activity at each habitat. M_b = body mass.

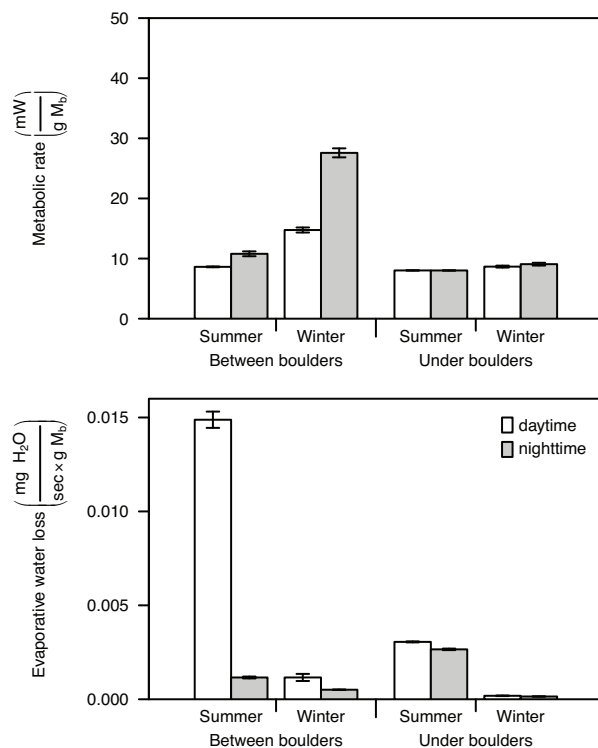


Figure 3: Hourly means (\pm SE) of individuals' (summer, $n = 5$; winter, $n = 6$) calculated energy expenditure and evaporative water loss during daytime (open bars) and nighttime (filled bars) foraging in the under-boulder and between-boulder microhabitats. M_b = body mass.

mice to use more efficient torpor during winter than during summer resulted in the lower field metabolic rates observed by Kronfeld-Schor et al (2001a) in the field, compensating for the higher foraging costs during the day in winter than in summer predicted by the model.

Thus, it appears that diurnal activity of golden spiny mice in their natural environment is optimal for energy conservation. This result may be explained, at least in part, by the structurally complex habitat in this rocky desert, where boulders create unique favorable microclimate conditions. Golden spiny mice are mostly active in the boulder habitat, where they are also relatively sheltered from avian and mammalian predators (Shargal et al. 1999, 2000; Jones and Dayan 2000; Jones et al. 2001; Mandelik et al. 2003). Foraging in the boulder habitat may also be advantageous in terms of resource availability: during three of four seasons, arthropods are more abundant in this habitat than in the open habitat, while in summer arthropods become more abundant in the open habitat (Vonshak et al 2009). Physiological considerations would suggest that spiny mice

should increase their foraging in summer in the UB microhabitat because of the high cost of evaporative water loss in the less sheltered BB microhabitat. Interestingly, previous research shows that in summer golden spiny mice tended to be more active and to forage to lower giving-up densities (GUDs) in less sheltered microhabitats between boulders and even in the open and reduced their foraging in the more sheltered and climatically less extreme UB microhabitat (Jones et al. 2001). This shift in use of foraging microhabitats counters that expected in response to daytime heat stress during summer, and the predictions of our model. Jones et al. (2001) hypothesized that it is driven by the saw-scaled vipers (*Echis coloratus*), active at Ein Gedi during the warm summer months. During the day, predation by vipers is a threat primarily under boulders, where these nocturnal sit-and-wait predators rest curled up. An additional force affecting foraging microhabitat use during summer may be the high arthropod availability (Vonshak et al. 2009). Thus physiological foraging costs in summer are expected to increase because foraging shifts in response to predation risk and possibly also arthropod abundance (Jones et al. 2001; Vonshak et al. 2009).

Previous work suggested that golden spiny mice shifted from their ancestral nocturnal activity phase to diurnal activity in response to competition by their nocturnal congener, the common spiny mouse (Shkolnik 1971; Gutman and Dayan 2005). Molecular phylogenetic research suggested that the golden spiny mouse lineage diverged approximately 6–8 million years ago, but the shift to diurnality occurred at the evolutionary scale about 0.3–0.5 million years ago, when it encountered the younger lineage of the common spiny mouse (Volobouev et al. 2007; V. Volobouev, personal communication). Amazingly, to this day golden spiny mice are active against their native nocturnal clock cycle (Levy et al. 2007).

These results raise the question of the evolutionary forces driving diurnality in golden spiny mice. Evolution is cumulative, and the conditions favoring the initial evolution of a trait and its subsequent maintenance need not be identical (Reeve and Sherman 1993). There are two major nonexclusive hypotheses to explain the current diurnal activity of golden spiny mice. The genus *Acomys* evolved as a savanna rodent of tropical Africa (Denys et al. 1994); hence it could be speculated that *Acomys* species developed adaptations to high ambient temperatures (including high evaporative water loss [Shkolnik and Borut 1969]) that preceded their adaptation to water shortage. Cohen and Kronfeld-Schor (2006) suggested that these adaptations enabled the golden spiny mouse to switch its activity into the thermoregulatory challenging diurnal niche upon encountering unfavorable conditions. These unfavorable conditions could be (a) low nocturnal am-

Table 2: Estimated effects of day part (night effect), microhabitat (under-boulder effect [UB]), and season (winter effect) on hourly mean energy expenditure and evaporative water loss during foraging according to the Bayesian statistical model

Dependent variable and fixed factor	Estimate \pm SD	95% CI
Energetic expenditure (mW/g M_b):		
Day part (night)	2.2 \pm .7	[.8, 3.5]
Microhabitat (UB)	-.6 \pm .3	[-1.1, -.1]
Season (winter)	5.9 \pm .3	[5.2, 6.5]
Day part \times microhabitat	-2.2 \pm .7	[-3.5, -.8]
Day part \times season	10.7 \pm .9	[8.9, 12.4]
Microhabitat \times season	-5.5 \pm .3	[-6.2, -4.8]
Microhabitat \times season \times day part	-10.3 \pm .9	[-12.1, -8.5]
Evaporative water loss (mg H ₂ O/s/g M_b):		
Day part (night)	-.0137 \pm .0006	[-.0150, -.0124]
Microhabitat (UB)	-.0118 \pm .0006	[-.0130, -.0106]
Season (winter)	-.0137 \pm .0006	[-.0150, -.0124]
Day part \times microhabitat	.0133 \pm .0006	[.0120, .0145]
Day part \times season	.0131 \pm .0006	[.0117, .0143]
Microhabitat \times season	.0109 \pm .0006	[.0095, .0121]
Microhabitat \times season \times day part	-.0127 \pm .0006	[-.0140, -.0113]

Note: Summer, $N = 5$; winter, $N = 6$. M_b = body mass. Significant factors have 95% confidence intervals (CIs) that do not span 0.

bient temperatures in the high mountains of the Sinai Desert, where the golden spiny mouse encounters no competition from congeners and yet is active during the day (Haim and Borut 1981), or (*b*) competition with common spiny mice in the Judean Desert population, the focus of our study. Over evolutionary time, golden spiny mice underwent further adaptations to activity during this phase of the diel cycle; consequently, in the absence of common spiny mice, golden spiny mice, even when able to exploit the night hours, remain primarily diurnal (Gutman and Dayan 2005). Thus, their current diurnal activity may reflect past selective forces to which golden spiny mice have now adapted; in the case of its interaction with the common spiny mouse one might invoke the “ghost of competition past” (Connell 1980).

The fact that model results show that golden spiny mouse physiology and habitat structure make diurnal activity energetically advantageous could suggest climate-driven diurnality is an alternative hypothesis to the competitive exclusion hypothesis in the Judean Desert; if golden spiny mice were already adapted to high ambient temperatures when the species arrived in the Judean Desert, diurnal activity of golden spiny mice in this region may have evolved regardless of competition, as appears to be the case in the Sinai Desert population. While we cannot refute this hypothesis, it seems less likely because (*a*) even under hot conditions in Africa, all other spiny mouse species remain nocturnal, and (*b*) while golden spiny mice may have already been heat adapted when arriving at the

Judean Desert, it is highly unlikely that they had already evolved adaptations for water retention before their arrival.

Be that as it may, our model results provide a simple and straightforward physiological explanation for the observation that golden spiny mice in the field remain primarily diurnal even in absence of common spiny mice (Gutman and Dayan 2005), while individuals in the lab, as well as field-captured individuals transferred to the lab, exhibit primarily nocturnal activity (Cohen and Kronfeld-Schor 2006; Levy et al. 2007; Cohen et al. 2009). Our model suggests that in the field, the climatic conditions golden spiny mice experience during the day are energetically favorable for activity. Thus, in spite of their nocturnal endogenous rhythms, night is not the energetically preferable temporal niche for golden spiny mice.

In sum, endotherm habitat-use models have previously been used to predict the spatial niche of species (e.g., Natori and Porter 2007). Here for the first time we explored the use of these models in predicting the fundamental temporal niche of diurnally active desert golden spiny mice. This model shows that diurnal activity is energetically favorable for spiny mice but that in summer there are prohibitive costs in evaporative water loss during midday. These results may explain (*a*) why golden spiny mice remain largely diurnal even in the absence of competition and (*b*) the trough in midday activity of golden spiny mice in summer. The model also shows that the boulder habitat provides not only shelter from avian and mammalian predators but also shelter from climatic extremes. How-

ever, risk of predation by vipers drives golden spiny mice into activity at less sheltered microhabitats during summer. We show that this shift imposes suboptimal conditions for golden spiny mice during summer; thus golden spiny mice pay a measurable physiological cost for avoiding predation by vipers. While climate is considered to play a major role in the physiology and evolution of mammals, this is the first study to model its potential to affect the evolution of activity patterns of mammals.

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